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THE MORPHOLOGY AND RELATIONSHIPS OF CIRCAEASTER

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THE PRESENT MORPHOLOGICAL STUDY of *Circaeaster agrestis* Maxim. was initiated because this plant is another example, in addition to *Kingdonia*, of an angiosperm with open dichotomous venation. This type of foliar vasculature is extremely rare in the dicotyledons and its taxonomic and phylogenetic significance raises very difficult problems which have recently been discussed in detail (Foster 1959, 1961a, 1961b; Foster & Arnott 1960). Throughout the long and vexed taxonomic history of *Circaeaster*, little attention has been given to its dichotomous venation and no attempt has been made to study possible fluctuations in the details of this pattern or to determine the existence of anastomoses or blind vein-endings. It is believed that the present study, based on the comparison of a wide range of leaf material, gives a fairly accurate picture of the trends of variation and demonstrates the often remarkable symmetry of the dichotomous pattern of venation.

In addition to the study of foliar vasculature, an effort was made to gain an accurate idea of the organization of the inflorescence and the morphology of the flower. This aspect of my investigation, supplemented by the embryological data provided by Junell (1931), has made it possible to review critically the various ideas which have been advanced regarding the systematic relationships of *Circaeaster*. It is my hope that the present article may serve to stimulate renewed interest in such relic genera as *Kingdonia* and *Circaeaster* and to demonstrate the fascinating evolutionary and taxonomic problems illustrated by the morphology of these herbaceous representatives of the Ranales.

DISTRIBUTION

The accompanying map (FIG. 1) reveals the extensive pattern of distribution of *Circaeaster* in Asia. Its present "range," to judge from the herbarium collections which I have examined, lies roughly along a curve extending from Kumaun through the Himalayas, southeastern Tibet, and northwestern Yunnan to the mountains of Kansu<sup>1</sup> and Shensi in north-

<sup>1</sup> This portion of China corresponds approximately to the "country" formerly called





FIG. 1. The distribution of *Circaeaster* and *Kingdonia* in Asia. Each solid dot (*Circaeaster*) or solid triangle (*Kingdonia*) indicates an approximate locality from which herbarium specimens were studied.

western China. The extremely few collections from Nepal, Sikkim, Szechuan, Kansu and Shensi do not necessarily indicate the infrequency of the genus in these areas. Further botanical surveys will very probably indicate a much wider and more continuous distributional pattern than is shown on the present map. Throughout its area of distribution, *Circaeaster* consistently occurs at relatively high altitudes which range from 8000–9000 feet in Shensi, Szechuan, and Sikang to 11,000–12,000 feet in Yunnan and Tibet. The highest altitude represented in any of the collections studied was 14,000 feet in Bhutan.

The data included on many herbarium labels gives some idea of the ecology of *Circaeaster* and the plants with which it is associated. It evidently prefers moist, shaded environments and has been found growing in habitats described as wet leaf mold under *Rhododendrons*; in the shade of a damp cave associated with bryophytes, *Circaea alpina* and other plants; forming large colonies on damp soil under *Hippophaë*; in open fir forest, etc. Despite its small size, *Circaeaster* must have considerable charm and attractiveness in nature, as illustrated by notes from a collection of *Polunin, Sykes, & Williams* in Nepal: "Growing in shallow soil on damp rock ledge. Stems pink. Leaves pale green. Filaments pale green, anthers brown. Ovaries green, with white hairs, stigma brown."

"Tangut" by the Mongols, a fact which explains Maximowicz's (1881, p. 557) reference to *Circaeaster* as "*herbula tangutica*" (see Prejevalsky 1876, 2: 301–302).



The map also indicates the much more restricted pattern of distribution of *Kingdonia*, a genus which Diels (1932) and Janchen (1949) assumed is closely related to *Circaeaster*. According to my limited information, both genera grow under very similar ecological conditions and it is interesting, and perhaps taxonomically significant, that their distribution coincides so exactly in northwestern Yunnan and in the mountains of Shensi and Kansu provinces (see map, FIG. 1). Future botanical explorations may result in the discovery of other localities for *Kingdonia* and thus remove the puzzle of its present apparent restriction to only two widely separated regions in China.

#### TAXONOMIC HISTORY

Specimens of the same kind of plant, later described and published as the genus *Circaeaster*<sup>2</sup> by Maximowicz in 1881, were discovered and collected about 1854 in Kumaun by the British botanists Strachey and Winterbotham. Their collections were sent to J. D. Hooker at Kew who prepared a drawing and an analysis of the plant for the Linnean Society. Unfortunately his data and the specimens were lost and in 1882 Hooker wrote to Mr. Duthie, who was to collect plants in the Himalayas, asking him to make an effort to find *Circaeaster* and emphasizing that "the plant is worth a pilgrimage, for I know nothing in the least like it" (see Huxley, 1918, p. 248). Duthie was successful in his search and his copious material, collected in Kumaun, enabled Oliver (1895) to prepare the detailed description and illustrations of *Circaeaster* which appeared in Hooker's *Icones Plantarum*.

During this early period of discovery and description, efforts were made to assign *Circaeaster* as an "anomalous genus" to some existing family in the dicotyledons. Maximowicz (1881), who based his description of the genus on specimens collected in 1880 in Kansu by Przewalski, was the first to suggest the possible affinities of *Circaeaster* with the Chloranthaceae. However, he confessed that its divergence in several respects might justify segregating it in a new family near the Chloranthaceae. Oliver (1895), on the other hand, expressed serious doubt as to Maximowicz's proposals and regarded *Circaeaster* "as a degraded form, allied perhaps to Anemoneae (Ranunculaceae)."

The disagreements as to the relationships of *Circaeaster* became intensified in subsequent taxonomic works and unfortunately were not always accompanied by additional studies on the actual morphology of the plant. On the one hand, Bentham and Hooker (1883) and Hooker (1890) followed Maximowicz and classified *Circaeaster* under the Chloranthaceae. Bentham regarded *Circaeaster* as "a very distinct genus but, it seems to us, with essential characters relating it to *Chloranthus* and indeed in its

<sup>2</sup> Maximowicz (1881) devised the name "*Circaeaster*" on the basis of the resemblance of its fruits with those of *Circaea* and because of the stellate disposition of the leaves. It is interesting to note that the vernacular Chinese name for *Circaeaster* is "Hsin Yeh Shu," literally "star-leaf herb" (How, 1958).



habit to some specimens of *C. japonica* Sieb." On the other hand, the affinities of *Circaeaster* with the Ranunculaceae were re-emphasized by Diels (1932) who based his decision upon the assumption that a close relationship exists between this genus and *Kingdonia*. The latter had previously been assigned to the Ranunculaceae by Balfour and Smith (1914). Diels's conclusions were later adopted without reservation by Janchen (1949) who segregated *Circaeaster* and *Kingdonia* as the two genera comprising the subtribe Kingdoniinae under the tribe Clematidae, subfamily Ranunculoideae of the Ranunculaceae.

These attempts to assign *Circaeaster* to either the Chloranthaceae or Ranunculaceae were in strong contrast with the efforts of other authors to segregate the genus in a new, independent family, the Circaeasteraceae. Post and Kuntze (1904) appear to have initiated this taxonomic treatment by suggesting that *Circaeaster* is either to be regarded as the sole genus in the subfamily "Circaeasterae" of the Chloranthaceae or as the representative of a distinct family, the Circaeasteraceae. Hutchinson, in both the 1926 and 1959 editions of his *Families of Flowering Plants* placed *Circaeaster* in the monotypic family Circaeasteraceae under the order Berberidales. Several other authors also accepted the family Circaeasteraceae. Hallier (1903), in his preliminary conspectus of flowering plants, included *Circaeaster* in the Ranunculaceae but later (1912) he grouped it under the family "Circaeastracées" in the order Ranales. Handel-Mazzetti (1931) located the family between the Ranunculaceae and Berberidaceae and Johansen (1950), following Hutchinson, classified it as a family under the Berberidales. Gundersen (1950), however, was less certain of the ordinal position of the family and apparently regarded *Circaeaster* as a possible genus to be included in the Berberidaceae.

Without question the detailed and meticulous investigations of Junell (1931) represent the most comprehensive morphological study of the past on *Circaeaster*. The living colony<sup>3</sup> of this plant which had been maintained for some years in the Botanical Garden at Upsala, Sweden, provided Junell with abundant material for his research on floral ontogeny, micro- and megasporogenesis, and the development of the gametophytes, endosperm, and embryo. Despite his expectations that an embryological study would shed new light on the vexed relationships of *Circaeaster*, this hope was not realized. In his skeptical opinion, "the systematic position of the plant is, on the contrary, about as uncertain as before." He correctly emphasizes that one of the inherent difficulties is the fact that the "life history" of those plants with which *Circaeaster* might be compared, is far too little known. This is certainly true with reference to *Kingdonia*, the embryology of which will continue to remain unknown until adequate preserved material can be obtained from China (see Foster, 1961a, p. 408).

<sup>3</sup> According to Junell, the plants grown at Upsala were obtained from the Botanic Garden at Edinburgh. That material originated, in turn, from collections of *Circaeaster* made in Sikkim in 1910 by W. W. Smith.



## MATERIALS AND METHODS

The material used as the basis for the present investigation was obtained from the following herbaria, the abbreviations for which are taken from Lanjouw and Stafleu's *Index Herbariorum*, Ed. 4, pt. 1. (Regnum Vegetabile 15. 1959): Arnold Arboretum of Harvard University, Cambridge (A), British Museum (Natural History), London (BM), Indian Botanic Garden, Calcutta (CAL), Royal Botanic Garden, Edinburgh (E), Conservatoire et Jardin botaniques, Genève, Switzerland (G), Herbarium, Royal Botanic Garden, Kew (K), Botanical Museum and Herbarium, Lund, Sweden (LD), Muséum National d'Histoire Naturelle, Paris (P), Naturhistoriska Riksmuseum, Stockholm (S), U. S. National Museum, Smithsonian Institution, Washington (US), and Botanical Research Station of Academia Sinica, Shensi, China (WUK). Grateful acknowledgement is made to the directors and curators of these herbaria for allowing me to remove leaf specimens, and in some cases entire plants, for my morphological studies.

The complete citations of the localities in China, Tibet and the Himalayas (see map, Fig. 1) where the specimens were collected are as follows: **China.** KANSU: *G. N. Potanin, s.n.* (P). SHENSI: Hsiang Sui Precipice, alt. 2800 m., *Liu 10678* (WUK). SIKANG: Kangting (Tachienlu) district, Chetola, alt. 3500 m., *Harry Smith 16936* (S); Chi-na-tung, Tsa-wa-rung, *Wang 65301, 65390* (A); Sacred Mountain, Kar-war-kar-loo, alt. 3400 m., *Wang 66252* (A). SZECHUAN: Karlang, alt. 3400 m., *Harry Smith 4141* (LD, S). YUNNAN: Western flank of the Lichiang Range, alt. 12,000 ft., *Forrest 6416* (E, K); moist rocky situations on the Chung-Tien plateau near Hsia-chung-Tien, alt. 12,000–13,000 ft., *Forrest 118* (E, K); *Handel-Mazzetti 8035* (US); "ad confines Tibeticas subjugo Dokerla," *Handel-Mazzetti 8035* (G); Anougu (Ngantschang), alt. 3550 m., *Handel-Mazzetti 7679* (P). **Tibet.** Tongolo, *Soulié 585* (G, P); Tongolo (Prin. de Kiala), *Soulié 355* (G, K); Kongbo Province, Sang La, Tsangpo Valley, alt. 12,000 ft., *Ludlow, Sherriff & Taylor 5033* (E); Kongbo Province, Hunket, Tumbatse, Rong Chu, alt. 11,600 ft., *Ludlow, Sherriff & Taylor 5033A* (E). **Bhutan.** Padima Tso near Thampe La, alt. 14,000 ft., *Ludlow, Sheriff & Hicks 17179* (E). **Sikkim.** Nuighil, alt. 13,000 ft., *W. W. Smith 4124* (CAL). **Nepal.** Bhurchula Lekh, near Jumia, alt. 12,000 ft., *Polunin, Sykes & Williams 4653* (BM); Suli Gad, between Rohagaon and Lulo Khola, alt. 10,000 ft., *Polunin, Sykes & Williams 3412* (BM); Langtang Valley, alt. 12,000 ft., *Polunin 1506* (BM); Rambrong, Lamjung, alt. 13,000 ft., *Stainton, Sykes & Williams, 6182* (BM). **Kumaun.** Amongst rocks under shade of trees near Saba Udigar in the Ralam Valley, alt. 8,000–9,000 ft., *J. F. Duthie 3354* (G); amongst rocks in the Ritur Valley, August 21, 1884, *J. F. Duthie, s.n.* (US 40004).

The descriptions and illustrations of foliar venation in this paper are based on material cleared with the aid of 2.5% NaOH and concentrated chloral hydrate, and stained with safranin. For the study and illustrations of the organography of the inflorescence and the structure and vasculature of the flowers, two methods were employed: (1) the outer portions of the leaves of a number of plants were first removed and the partly defoliated specimens then cleared and stained by the same techniques used for studying leaf venation; and (2) some of the defoliated plants (includ-



ing the upper part of the hypocotyl) were cleared and then dehydrated by the tertiary butyl alcohol method, infiltrated with "Histowax," sectioned transversely at 7–8 $\mu$  in thickness, and stained with a combination of safranin and light green. Because of the very small size and crowded arrangement of the numerous flowers, serial transections proved indispensable in the reconstruction of the morphology and vasculature of the remarkable inflorescence of *Circaeaster* (see FIG. 30a–d).

Thanks are due to Mr. Nels Lersten for his assistance with the processing, sectioning and staining of some of the inflorescence material and to Miss Charlotte Mentges who prepared the outline map represented in FIG. 1. The photomicrographs of leaf venation and the transections of the inflorescence were made by Mr. Victor Duran and the line drawings prepared by Mrs. Emily R. Reid. Appreciation is also due to Dr. Shiu-ying Hu, of the Arnold Arboretum, Harvard University, for translating into English the descriptions of *Circaeaster* and *Kingdonia* found in the recent treatise on Chinese plants by How (1958), to Dr. Rimo Bacigalupi and Professor Arthur E. Gordon for their assistance with the Latin description in Maximowicz's (1881) article, and to my wife for her help in proof-reading the manuscript.

This paper was written during my appointment as Miller Research Professor at the University of California for the academic year 1962–63. It is a pleasure to express my thanks for the opportunity for study provided by this appointment.

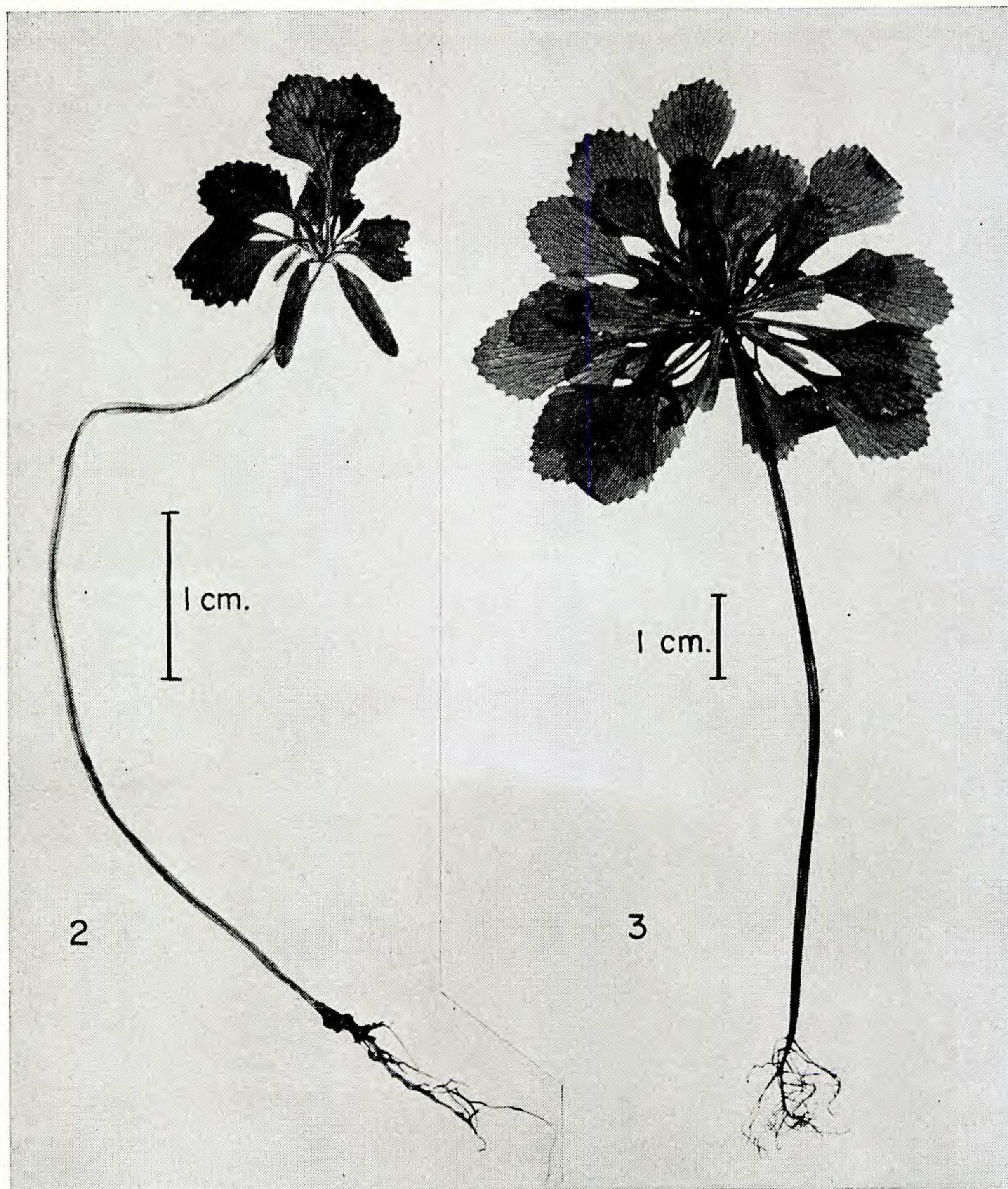
#### GENERAL ORGANOGRAPHY

Plants of *Circaeaster* are annual herbs with a very distinctive and unusual habit of growth. The elongated axis is the result of the exaggerated development of the hypocotyl which bears at its summit, below the rosette of crowded leaves, a pair of linear and persistent cotyledons (FIGS. 2–3). Junell (1931) studied the early phases of germination and his Figure 7e shows clearly the early and conspicuous elongation of the hypocotyl of the young seedling. Troll (1938, p. 1093 footnote) compared the growth-form of *Circaeaster* with the "little-tree rosette" ("Bäumschenrosetten") habit of certain species of *Biophytum* (Oxalidaceae). In *B. sensitivum*, for example, the general organography of a flowering specimen, as depicted by Troll (1937, p. 222, Abb. 141) is remarkably similar to a mature specimen of *Circaeaster*, despite the obvious differences in leaf form.

Although the hypocotyl of *Circaeaster* may reach a length of 8 cm. or more in vigorous specimens, it is difficult to determine from the vague statements in the literature whether the rosette of leaves, is borne in an upright or a prostrate position in nature. Junell (1931), with an opportunity to study living plants in cultivation, merely states that the plant has "an upright, unbranched, smooth stem." It seems possible, however, that in some cases the hypocotyl may remain buried in the moss or the leaf mold in which the plant frequently grows in its natural habitat.

The development of an individual plant of *Circaeaster* is terminated by

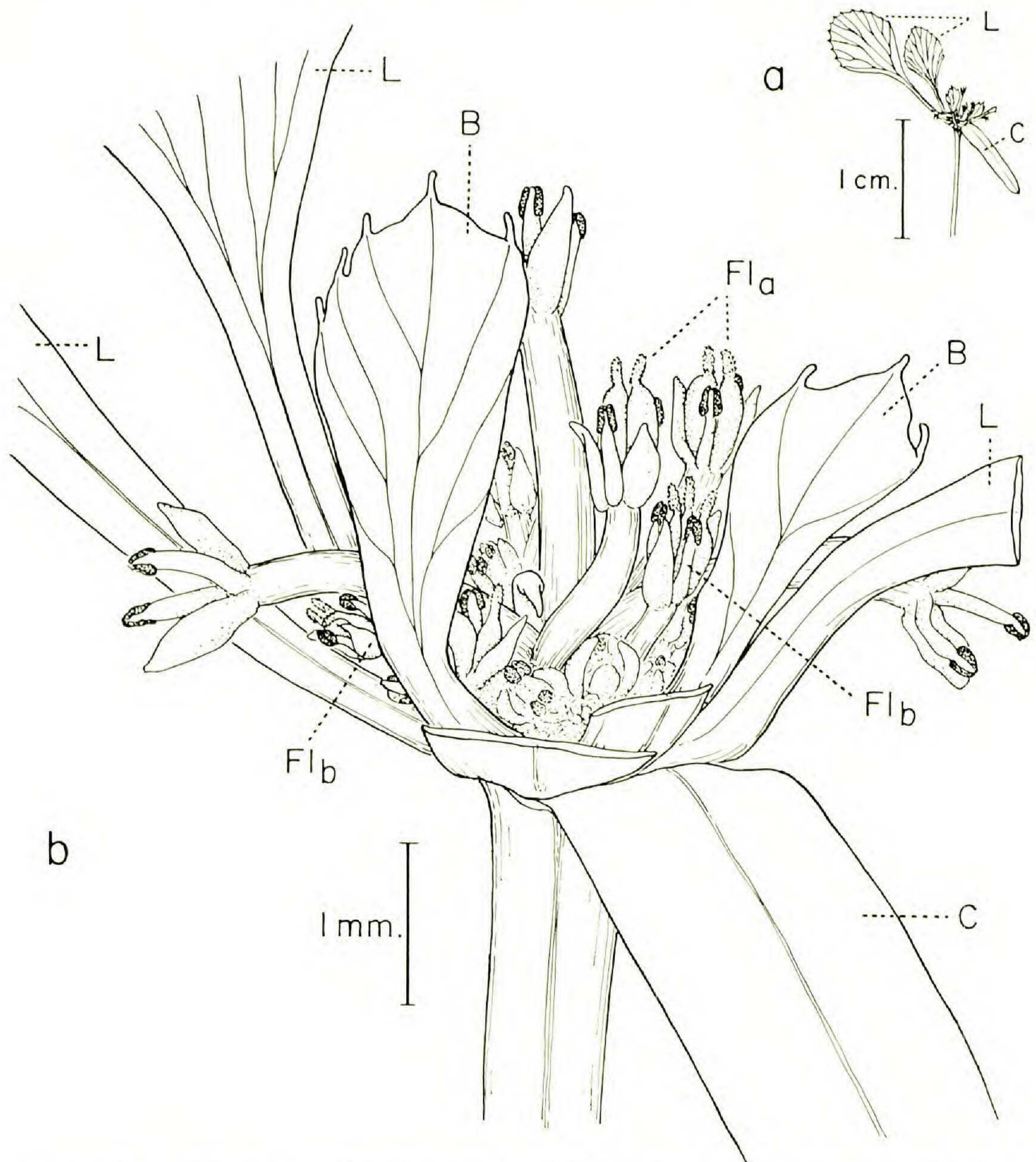




FIGS. 2 and 3. General organography and habit of *Circaeaster*. 2, specimen showing the typical elongated hypocotyl, the pair of persistent cotyledons and, just above the left cotyledon, a maturing hairy fruit (*Wang 65930, A*). 3, a very robust plant from the living collection at Upsala (*Junell s.n., P*). Note the cotyledons, primary leaves, and the conspicuous pattern of open dichotomous venation.

the formation, in the center of the rosette of leaves, of a condensed terminal inflorescence composed of numerous minute flowers (FIG. 4). Flowers, in the most varied stages of development, may occur at the same time in a given individual. Following pollination, the very slender pedicels of many of the flowers elongate and bear at their tips one or more fruits (with their characteristic uncinata hairs), together with the persistent tepals and the remains of the stamens (FIGS. 34–35).





FIGS. 4a and b. Cleared and partially defoliated specimen showing the fasciculate arrangement of the flowers in the terminal inflorescence. (*Stainton, Sykes & Williams 6182, BM*). 4a, low power view, emphasizing minute size of flowers; 4b, greatly enlarged view of same. Note elongated pedicels of flowers in center of inflorescence and the occurrence of both bi- and tricarpellate flowers. B, bract; C, cotyledon; Fla, bicarpellate flower; Flb, tricarpellate flower; L, foliage leaf.

#### MORPHOLOGY AND VASCULATURE OF LEAVES

**Phyllotaxis.** The foliar organs of a mature specimen of *Circaeaster* consist of two linear cotyledons, a variable number of small petiolate foliage leaves and the bracts which subtend the peripheral fascicles of flowers of the abbreviated inflorescence (Figs. 30a–b). These appendages, however, are so crowded in their attachment to the stem that it is very difficult, without an ontogenetic study, to determine whether the phyllotaxis is decussate, whorled, or spiral. Junell (1931) examined the sequence of leaf-primordia formation in four seedlings but encountered such



variability that he reached no firm conclusion. FIG. 30a supports his observation that the two cotyledons do not lie in the same plane; it also shows that the position of the six leaves and five bracts might be interpreted as the result of a slightly "distorted" pattern of decussate phyllotaxis.

**Nodal Anatomy.** Serial transections reveal that the vascular system of the upper end of the hypocotyl is a diarch primary xylem plate flanked on each side by two well-developed collateral strands of secondary phloem and secondary xylem. At the level of attachment of the cotyledons, each of these appendages is vascularized by a trace which diverges from a corresponding protoxylem pole. The xylem portion of each cotyledonary trace is often composed of two closely spaced strands of tracheary elements while the phloem appears as a continuous strip of tissue. Two similar traces, derived from the remainder of the primary xylem plate, extend into the bases of the first "pair" of foliage leaves, which lie approximately at right angles to the plane of the cotyledons.

At this level of section, a division of the collateral strands of secondary vascular tissue occurs and produces four large bundles; the center of the axis is now represented by a parenchymatous pith. The single traces of the remaining foliage leaves seem to originate as branches of these four major components of the highly condensed "eustele." FIG. 30a-d shows that the xylem of each leaf trace is often conspicuously double at various levels in its extension through the petiole.

The accurate reconstruction of the vasculature of the axis is complicated by the common origin of leaf and bract traces or bract and pedicel traces from the same major bundle of the stele. Moreover, it has not been possible, with the very limited study of "revived" herbarium material to discover the origin and the basal interconnections of the vascular systems of the central flowers. Unfortunately Junell (1931), with abundant fresh material at his disposal, apparently made no attempt to reconstruct the remarkable vasculature of the shoot or inflorescence of *Circaeaster*.

**Form and Venation of Cotyledons.** The cotyledons of *Circaeaster* are linear or strap-shaped appendages and vary in size from 7-10 mm. in length and 1.5-3 mm. in maximum width. In contrast with the dichotomously veined lamina of the foliage leaves, the entire cotyledon is traversed by an unbranched midvein which represents the upward extension of its single trace (FIGS. 2, 6). Careful study of cleared preparations indicates that the xylem of the midvein, at various levels or throughout its course, consists of two closely approximated strands of tracheids which may separate as two very short endings below the blunt apex of the cotyledon (FIG. 6). Serial transections confirm the fluctuation in the degree of doubleness of the xylem at various levels (FIGS. 30a-d, cotyledon at left).

**Form and Venation of Foliage Leaves.** The foliage leaves are



clearly demarcated into petiole and lamina; the latter varies from broadly spatulate to rhomboidal in form and is provided with small mucronate dentations at its distal margin (Figs. 5, 7-13, 15-29). Considerable fluctuation was observed in the size of the leaf, not only between plants from different collections but also between the successive leaves in a single rosette. The largest leaves studied measured about 30 mm. in length with a maximum lamina diameter of 16-17 mm. (*Liu 10678*, WUK). At the opposite extreme, the very small leaves shown in Figs. 7-11 are all less than 7 mm. in length and measure only 2.25-3.5 mm. in lamina width. Leaves from other collections were somewhat intermediate in their dimensions between these two extremes.

Although the distinctive pattern of open dichotomous venation is superficially evident even in dry herbarium specimens, the few descriptions of the foliar vasculature in the literature are very brief and in part inaccurate. The first specific description of dichotomous venation in *Circaeaster* was given by Oliver (1895) who stated: "The petioles, like the hypocotyledonary axis, are traversed by a solitary vascular bundle which repeatedly forks in the lamina giving off a branch to each serrature." Junell's (1931) description is similar but slightly more detailed. He found that the petiolar bundle divides into two or three branches, the median one of which often does not divide further. "Finer lateral veins are not present" and in the colony of *Circaeaster* grown at Upsala, the leaves had on the average 14 teeth with a corresponding number of vein endings. No additional information on leaf venation is found in Diels's (1932) paper and Troll (1938) merely attempted, on purely theoretical grounds, to argue that the dichotomous venation of *Circaeaster* represents a secondary "modification" of pinnate venation. In none of these descriptions is reference made either to blind vein-endings or to anastomoses, examples of which were encountered in the present survey (Figs. 23-29). The descriptions and illustrations given in the present paper indicate a wide variation in the *details* of the venation pattern in *Circaeaster* and are based on the study of 97 cleared leaves derived from a total of 24 different herbarium collections.

In many of the plants studied, the cotyledons are followed by a series of 2 or more small leaves with extremely simple patterns of dichotomous venation (Figs. 7-9, 12, 13, 15, 16). For convenience, these leaves will be designated as "primary" or "juvenile leaves" although it is recognized that there is no clear morphological demarcation between them and the succeeding more highly vascularized foliage leaves. A striking example of a gradual progressive elaboration of dichotomous venation is shown in the leaf series represented in Figs. 7-11. Each of the three very small "primary leaves" is vascularized by a trace with double xylem, which extends through the short petiole and dichotomizes near the base of the lamina (Figs. 7-9). The dichotomous branching of the two basal veins in the first leaf occurs at about the same level and yields four vein-endings which terminate below corresponding marginal teeth (Fig. 7). In the second leaf with five vein-endings, dichotomy of the basal veins occurs



at different levels producing a "midvein" and two dichotomized lateral veins; the branch of one lateral, however, terminates blindly without a corresponding marginal tooth (FIG. 8). In the third primary leaf, three symmetrical pairs of vein-endings have been produced by the dichotomy, at nearly the same level, of the central and the two basal lateral veins (FIG. 9). This leaf is followed by two larger appendages, with eight and nine vein-endings respectively, terminating below corresponding teeth (FIGS. 10-11). The increase in number of veins in these organs has resulted from further symmetrical or asymmetrical branching of the lateral vein-systems.

The primary leaves of other collections are notable because of the prominence of an unbranched "midvein" which traverses the central region of the lamina (FIGS. 12-13, 23). Appendages of this type tend to develop an odd rather than an even number of vein-endings. Most commonly, the midvein originates as the inner of the two veins formed by the dichotomy of one of the main xylem strands of the petiolar bundles. In a few cases, however, the midvein is formed by the union of the two central bundles produced by the dichotomy — at different levels — of each of the two xylem strands in the upper region of the petiole (FIG. 14). From a broad comparative viewpoint it is interesting to note that both of the types of midvein origin found in the primary leaves of *Circaeaster* also occur in the dichotomously veined tepals of the flower of *Kingdonia* (Foster 1961a, plate 1).

The increasing complexity of the venation in successive "primary leaves" of a plant reaches its culmination in the elaborate patterns of dichotomous venation found in well-developed foliage leaves (FIGS. 5, 17-29). Profuse and often very regular dichotomous branching of the veins imparts an elegance and a symmetry to the various patterns which may now be examined in some detail.

The *degree* of symmetry of the venation pattern appears closely associated with (1) variations in the number of main veins in the lamina base and (2) the patterns and levels of successive dichotomous branching in each of the principal systems of veins. Very commonly a central and two main lateral veins diverge at nearly the same level in the lamina base; as in the primary leaves, the central vein is produced by the division of one of the two main xylem strands of the petiolar bundle. In leaves with this type of basal vasculature, the successive dichotomous branching of the central and both lateral veins may be extremely regular, resulting in an even number of vein-endings (FIGS. 5, 19). Essentially similar patterns, but with an odd number of vein-endings are formed if certain of the distal veins fail to dichotomize before terminating at the margin (FIGS. 20, 24, 27).

Transitions to a more isotomous type of basal vein-dichotomy were also encountered in the present survey. In these cases, *each* of the two xylem strands of the petiolar bundle tends to dichotomize at a low level in the lamina base yielding four or sometimes five main veins. The pattern of dichotomous branching of these veins is variable, however, and produces



either an odd (FIGS. 18, 21) or an even (FIG. 22) number of marginal vein-endings. A distinctive feature of the leaf shown in FIG. 18 is the divergence, from one of the basal vein-dichotomies, of a long unbranched central vein which resembles the "midvein" in primary leaves (cf. FIGS. 12, 13, 18 and 23). This venation pattern was observed in a few of the foliage leaves from a cultivated specimen of *Circaeaster* (*Junell s.n.*, P). Usually the "central vein" in foliage leaves branches dichotomously at some level in the lamina (FIGS. 5, 19-22, 24).

The only examples of a strictly isotomous pattern of basal venation were found in the leaves of a specimen from the Shensi collections (*Liu 10678*, WUK). In these appendages a central vein system is not formed and the vasculature of the two halves of the lamina is derived from the pair of veins produced by the *equal division* of the petiolar bundle (FIGS. 15-17). In the larger primary leaf and the foliage leaf which follows it, the isotomous branching is repeated at the same level by each of the two main veins (FIGS. 16, 17). The venation of the smaller primary leaf (FIG. 15) is the simplest pattern encountered in the present study and is highly suggestive of a "transition" between cotyledonary and foliage-leaf venation (cf. FIGS. 6 and 15).

In the majority of the leaves examined, *all* the vein-endings terminate in corresponding marginal teeth. This type of one-to-one correlation seems to predominate regardless of the degree of symmetry of the venation pattern or the form or size of the lamina.<sup>4</sup> Careful study, however, has revealed that in addition to this normal pattern of marginal venation, the leaves of a few collections possess blind vein-endings, i.e., veins which terminate in various positions distal to the lamina margin (FIGS. 8, 22-26). Usually only one or two leaves of a given plant form veins of this type and their occurrence in either primary leaves or the larger foliage leaves is sporadic and unpredictable. Frequently only a single blind vein-ending may develop in an otherwise regular pattern of dichotomous venation. In these instances it is usually obvious that such a vein represents the shorter of the two branches derived from a dichotomy (FIGS. 22, 24). The most consistent and profuse development of blind vein-endings was observed in a series of plants from one of the collections from Nepal (*Stainton, Sykes & Williams 6182*, BM). Out of a total of 24 leaves examined, 16 showed blind endings located at various points in the venation (FIGS. 25, 26). In one of these leaves (FIG. 25) there are three blind terminations, each of which clearly represents an "overtopped" branch of a dichotomized system of veins. A similar morphological interpretation seems valid for the four delicate and much shorter vein-endings shown in FIG. 26.

Possibly the apparent infrequency of blind vein-endings observed in *Circaeaster* is merely the result of insufficient sampling. But it is interest-

<sup>4</sup> In a few of the leaves examined, one of the marginal teeth (usually the outermost one in the series) is vascularized by a strand of xylem which is unconnected with the xylem of the adjacent vein. Discontinuous strands of this type raise interesting ontogenetic questions which, however, could not be solved by the study of cleared leaves of herbarium specimens.



ing that in the much larger dichotomously veined leaves of *Kingdonia*, blind endings are relatively numerous and occur in all the specimens which were studied (Foster & Arnott 1960, p. 695, Table I). Until ontogenetic studies have been made on the leaves of the two genera, however, the full morphological significance of blind vein-endings in the open dichotomous venation patterns must remain a question.

Throughout the present investigation a very careful search was made for vein anastomoses. They proved to be extremely infrequent and only four examples were encountered in my survey of nearly 100 leaves. Only a single anastomosis occurs in each case and its position in the venation pattern varies from leaf to leaf (Figs. 28, 29). As in *Kingdonia* the anastomoses represent fundamentally the union between the adjacent branches of two vein-dichotomies. Fig. 27 shows an interesting example of the close approximation, without fusion, between the inner and nearly equal branches of two veins which have dichotomized at about the same level. In another leaf from a different collection (*Soulié 585, p*) a similar pattern was observed except that the two veins were anatomically joined for a very short distance before their divergence as two separate strands. In each of the anastomoses shown in Figs. 28, 29, however, the two inner branches which unite are conspicuously unequal in length and degree of development. The shorter and more slender branch (consisting of a single file of tracheids) joins its neighbor either near the level of a vein-dichotomy (Fig. 28) or at a much higher point (Fig. 29). In both cases, the areoles which result are characteristically elongated and closely resemble those produced by similar vein-unions in *Kingdonia* (Foster 1959, pl. 2).

### INFLORESCENCE

The minute and numerous flowers of *Circaeaster* are aggregated in a compact terminal inflorescence which occupies the center of the "rosette" of leaves (Figs. 4, 30). Although cleared and partly defoliated specimens are useful in showing the fasciculate arrangement of the flowers and the small dichotomously veined bracts, the complex organization of the inflorescence is fully revealed only by the study of microtomed serial transections. These are difficult to secure because the short epicotylar axis is frequently bent or excessively compressed in herbarium specimens. The description which follows is based on the study of the relatively few satisfactory transectional series which were obtained.

FIGURES 30a-d represent a series of transections of an inflorescence composed of 28 flowers. The majority of the flowers are disposed in five peripheral fascicles and each fascicle is subtended by a small bract (Figs. 30a and b, flower-groups subtended by bracts B1-B5). The fascicles are numbered according to the length of their associated bracts, number 1 having the longest bract (661 $\mu$ ) and number 5 the shortest (152 $\mu$ ). It is uncertain whether this sequence indicates an ontogenetic succession but it should be noted that each bract and its subtended fascicle occurs *between* the bases of two adjacent foliage leaves. Most of the flowers in the



peripheral fascicles are in very early stages of development but in three fascicles the largest flower was sufficiently mature to have ripe pollen or primary sporogenous tissue in the anthers (FIG. 30c, flowers subtended by bracts B1, B3, B4). In some fascicles, the flowers are collaterally arranged and basally joined to form a very short stalk or "peduncle" adnate to the bract (FIG. 30a, B4).

The five largest and best developed flowers in this inflorescence are devoid of bracts and collectively represent a central fascicle. Beginning at the base of this fascicle, the elongated pedicels of flowers V, IV, III and II progressively become free, and flower I (with the longest pedicel and most highly developed carpel) morphologically represents the terminal flower of the entire inflorescence (FIGS. 30a-d).

Transections of the inflorescence of several other specimens revealed a similar general type of morphology but showed that the number of flowers in the peripheral fascicles may consistently be reduced to two. In a plant collected in Yunnan (*Forrest 6416*, E) each bract subtends a pair of basally united flowers, one pedicellate and well developed, the other small and rudimentary. It seems possible that only the larger flower in each of these fascicles may be functional. Similar examples of two-flowered fascicles were found in studying serial transections of the inflorescence shown in FIG. 4. The possible significance of this divergence from the many-flowered fascicles illustrated in FIGS. 30a and b can only be determined by the comparison of a much wider range of material than I have been able to assemble.

Very few efforts have been made in the past to interpret or to classify the peculiar and distinctive inflorescence of *Circaeaster*. Maximowicz (1881) observed the association of small hyaline bracts with the bases of the flower pedicels and stated that the "very minute flowers are fascicled in the upper axils forming a many-flowered terminal inflorescence." Bentham and Hooker (1883) were more explicit; they regarded the inflorescence as a small raceme "reduced to a fascicle with the common rachis scarcely or not at all developed." Oliver (1895) characterized the arrangement of the floral pedicels as "umbellate-fasciculate." In the modern period the morphological and taxonomic significance of the inflorescence has been entirely ignored by Diels (1932), Janchen (1949), and Hutchinson (1959). As far as I can discover, Junell (1931) is the only investigator to propose an interpretation of the inflorescence based upon its methods of development. Using longitudinal sections he found that the order of flowering is centrifugal and concluded that "*Circaeaster* apparently has a cymose inflorescence."

In the light of the present study it is difficult to decide whether the inflorescence of *Circaeaster* is morphologically equivalent to either a reduced cyme or to a raceme. From a speculative viewpoint it is possible to imagine that excessive phylogenetic reduction of an originally cymose or racemose terminal inflorescence has occurred, resulting in the elimination of all bracts except those which subtend the peripheral fascicles of flowers. But until the taxonomic affinities of *Circaeaster* have been fully



clarified, the evolution of its peculiar inflorescence will continue to remain an intriguing but unsolved problem.

#### MORPHOLOGY AND VASCULATURE OF FLOWERS

The minute apetalous hermaphroditic flowers of *Circaeaster* are highly variable with respect to the number of tepals (T), stamens (S), and carpels (C) which they develop and the total range in variation observed in this study may be summarized by the formula  $T^{2-3}$ ,  $S^{1-3}$ ,  $C^{1-3}$ . Variation is extensive not only between flowers of different collections but even among the flowers of the same inflorescence. For example, in both of the collections from Tibet (*Soulié* 355, p, g), the majority of the flowers in the inflorescence consist of 3 tepals, 1 stamen and 1 carpel (FIG. 30c, peripheral flowers of bracts B1, B3, B4; FIG. 30d, central flower IV); one of the central flowers in each inflorescence, however, has 2 tepals, 2 stamens, and 1 carpel (FIG. 30d, flower V). This latter pattern, which was apparently regarded as "typical" for the genus by Maximowicz (1881) and Hutchinson (1959) is infrequent in my material and I have only observed it, in addition to the cases just noted, in the flowers of the peripheral fascicles of the inflorescence of a collection by Forrest (6416, E). In some collections, bi- and tricarpellate flowers appear to predominate and both types occur in the same inflorescence (FIG. 4, f1<sub>a</sub>, f1<sub>b</sub>). The most unusual flower encountered consists of 3 tepals, 3 stamens, and 3 carpels (FIG. 33). This flower, which appears perfectly "normal" in structure, occurs in an inflorescence largely composed of flowers with 2 tepals, 2 stamens and 2 carpels.

The vascular system of the flower pedicel consists of one or two strands of narrow tracheids flanked by two bundles of phloem; in many cases, the phloem appears to surround the xylem giving the appearance of a typical "protostele." Near the level of attachment of the floral organs, two important structural changes are evident: (1) an active cambial zone develops beneath the phloem tissue and (2) the previously slender strand of xylem abruptly dilates and now consists of a mass of short tracheids with enlarged lumina. Each of the single traces of the tepals, stamens and carpels diverges from this central "nest" of tracheids but "revived" herbarium material was too poor in quality to permit an accurate reconstruction of the vasculature of the floral receptacle (see semidiagrammatic representations in FIGS. 31-35).

In cleared material, the persistent scale-like tepals often appear devoid of vasculature and serial transections reveal that the single weak trace may end below or at the base of these appendages. In more robust specimens, however, the upward extension of the trace forms a midvein containing a very delicate unbranched strand of xylem.

The stamens of *Circaeaster* are distinctive in structure because only one pair of introrse microsporangia is developed. Dehiscence is longitudinal and very small tricolpate pollen grains have frequently been observed adhering to the elaborate papillae of the stigma (FIG. 31). Each



stamen is vascularized by a single median vein which terminates below the narrow connective separating the pair of microsporangia (FIGS. 31–35).

Each of the carpels is vascularized by a well-developed amphicribal trace which divides near the base of the ovary into a dorsal and a ventral vein (FIGS. 32–34). These two strands constitute the total vasculature of the carpel and no additional venation is developed as the carpel matures into a fruit. The dorsal bundle extends up the convex abaxial side of the carpel and ends below the base of the papillate stigma. The ventral vein traverses the adaxial side of the carpel and according to Junell (1931) passes through the massive funiculus of the single functional ovule and terminates at the chalazal end of the embryo sac.

The enlargement of a carpel into a fruit is accompanied by the profuse development of unicellular hairs which are conspicuously hooked at maturity (FIGS. 34, 35). These trichomes are progressively initiated in a basipetal sequence from the ovary wall and first appear in an area well below the terminal stigma (FIGS. 32, 33). As a result, the upper end of the mature fruit remains entirely glabrous (FIGS. 34, 35). I have never observed any example of the completely or partially glabrous fruits which Handel-Mazzetti (1931) and Junell (1931) noted in certain collections. Hooker (1890) emphasized the possible role of the uncinata hairs in the dispersal of the fruits and believed that they are “such aids to dispersion that it [i.e., *Circaeaster*] may be supposed to be common though so inconspicuous as to be overlooked.”

#### DISCUSSION

In the more than 80 years that have elapsed since the establishment of the genus *Circaeaster* by Maximowicz (1881), no general agreement has been reached as to the systematic affinities of this peculiar genus. A considerable part of the controversy has been due to the exploitation of a very few selected morphological features for *direct* comparison with presumably homologous characters in members of such families as the Chloranthaceae, Ranunculaceae and Berberidaceae. Unfortunately this practice has been based to some extent on an inaccurate, or at the very least, an inadequate understanding of the floral morphology of *Circaeaster*. Furthermore, when the *combination* of highly remarkable morphological and embryological characters of *Circaeaster* is fully appreciated and compared with the situation in the suggested relatives of *Circaeaster*, the “anomalous” position of the genus is emphasized and justification is provided for its segregation in the monotypic family Circaeasteraceae. In the light of the present investigation, supplemented by the embryological data provided by Junell (1931), the various proposals for classifying *Circaeaster* may now be critically examined.

The possible relationship of *Circaeaster* to the family Chloranthaceae in the Piperales was first suggested by Maximowicz (1881) and his viewpoint was later adopted for the Bentham and Hooker (1883) system of



classification. As far as I can determine, this taxonomic treatment was fundamentally based on the assumption that the flower of *Circaeaster*, like that of members of the Chloranthaceae, is unicarpellate and that the ovary contains a single, pendulous orthotropous ovule. While it is true that unicarpellate flowers commonly occur in *Circaeaster*, there is considerable variation even between flowers of the same inflorescence and gynoecia composed of 2 or 3 carpels have been encountered frequently in the present investigation (Figs. 4, 31–33). But in addition to the divergence in carpel number, the presumed relationship between *Circaeaster* and the Chloranthaceae is negated by the following additional contrasts: (1) *pollen*, tricolpate in *Circaeaster* (Erdtman 1952), monocolpate, acolpate or polycolpate in the Chloranthaceae (Swamy 1953); (2) “*ethereal oil cells*” (i.e., secretory idioblasts) absent in *Circaeaster* (Schulze 1900, Solereder 1908, Metcalfe & Chalk 1950), present in all genera of the Chloranthaceae (Swamy 1953); (3) *vessel members*, with simple perforations in *Circaeaster* (Cheadle 1953, p. 34), with scalariform perforations in all members of the Chloranthaceae (Swamy 1953); (4) *foliar venation*, open dichotomous in *Circaeaster*, pinnate-reticulate in the Chloranthaceae (Swamy 1953); (5) *pollen tube*, mesogamous in *Circaeaster* (Junell 1931), porogamous in the Chloranthaceae (Schnarf 1931); (6) *endosperm*, cellular and of the *Adoxa*-type in *Circaeaster* (Junell 1931), cellular, the first walls predominantly transverse in *Hedyosmum* of the Chloranthaceae (Swamy 1953). In connection with these contrasts, it is interesting to note that Junell (1931) found two points of resemblance between *Circaeaster* and the Saururaceae, a family included with the Chloranthaceae and Piperaceae in the order Piperales (Hutchinson 1959). According to Junell, the genus *Saururus*, which usually has 3–4 free or basally joined carpels, shows “great similarity” to *Circaeaster* in that in both genera, *two* orthotropous ovules begin development from the inner surface of the carpel but only one of them becomes fertilized and forms the single seed. However, as Junell admits, an important difference between the two genera is the development of a massive perisperm in the seeds of *Saururus*. A further divergence, in my opinion, is the unusual formation of the *Adoxa*-type of endosperm in *Circaeaster*.

With reference to the Ranales (*sensu lato*), the possible affinity of *Circaeaster* with the Ranunculaceae was originally suggested by Oliver (1895) but he gave no morphological evidence to support his conjecture. Diels (1932), however, strongly insisted that *Circaeaster* should be regarded as the most extremely reduced member of the Ranunculaceae and that its closest affinities are with *Kingdonia* which had already been classified as a new genus in this family by Balfour and Smith (1914). The two main points of resemblance between *Circaeaster* and *Kingdonia* used by Diels to support his argument are the presence of a solitary, orthotropous, pendulous ovule and the dichotomous venation of the leaves. In the light of our present knowledge, these points of agreement are clearly not decisive in the determination of the correct systematic position of *either* genus (Foster 1959, 1961a). To judge from the recent studies of Bersier



(1960), Vijayaraghavan (1962) and Bhandari (1962), the ovule in a variety of genera of Ranunculaceae is typically anatropous, and there is no evidence that the orthotropous pendulous ovule of either *Circaeaster* or *Kingdonia* has arisen as a "modification" of this feature. As Swamy (1953) pointed out in discussing the relationships of the Chloranthaceae, "the very fact that orthotropous ovules occur in many unrelated families suggests that its development may as well be due to parallel evolutionary trends." The use by Diels (1932) of dichotomous venation as indicating the affinity between *Circaeaster* and *Kingdonia* and hence justifying the assignment of these genera to the Ranunculaceae, seems particularly unconvincing. As I have discussed in detail in several recent papers, the unilacunar node, the four leaf traces and the palmate open dichotomous venation of the leaf of *Kingdonia* are not duplicated, as far as I can determine, in any of the generally recognized genera of the Ranunculaceae (Foster 1959, 1961a). A similar objection arises to the use of the unifasciculate leaf trace and open dichotomous venation of *Circaeaster* in supporting the family relationships of this genus with the Ranunculaceae (Figs. 5, 7-13, 15-29). In this connection it should be emphasized that the investigations of Sterkx (1900) revealed that even the cotyledons of a wide range of ranunculaceous genera develop relatively complex net venation. In place of a *divergent* and open dichotomous pattern of branching, the main lateral veins *converge* towards the leaf apex and join the well-defined midvein (see also Höster & Zimmerman 1960 and Höster 1962).

It is a curious fact that although Janchen (1949) fully agreed with Diels's taxonomic conclusions, he made no reference to the highly distinctive venation of *Kingdonia* and *Circaeaster*. His precise assignment of these two genera to the tribe Clematideae in the Ranunculaceae was based on the absence of nectariferous leaves, the uniovulate carpels, and the pendulous ovule. Janchen concluded that because of the form of their leaves (simple or palmately divided) and the herbaceous character of the plants, the subtribe Kingdoniinae comprising *Circaeaster* and *Kingdonia* must be regarded as "a secondarily simplified group, derived from Anemoninae-like ancestors." This speculation, however, is not supported by several of the "unique" features revealed by Junell's (1931) embryological study of *Circaeaster*: (1) the mesogamous course of the pollen tube and (2) the *Adoxa*-type of endosperm development. Although cellular endosperm is characteristic of a number of woody ranalian families (Swamy 1953, Swamy & Bailey 1949), the endosperm in all investigated members of the Ranunculaceae is nuclear in type (Schnarf 1931). In this connection, it should be mentioned that Swamy and Ganapathy (1957) concluded that the "Nuclear-type endosperm is in all probability more advanced than Cellular-type endosperm." If this idea is valid, it is difficult to imagine that the distinctive and very rare *Adoxa*-type of endosperm of *Circaeaster* is the result of phylogenetic derivation from the nuclear type characteristic of the Ranunculaceae as a whole.

When the *totality* of evidence from foliar vasculature, anatomy, inflorescence and flower, and the embryology is weighed and compared, there



appears to be no convincing evidence for retaining *Circaeaster* as an "anomalous" genus in any of the families which have just been discussed. On the contrary, I fully agree with Hutchinson's (1959) placement of the genus in an independent monotypic family, the Circaeasteraceae, although I cannot accept the major characters he employs to classify this family under the order Berberidales. In his key to the six families which he includes in this order, Hutchinson separates the Circaeasteraceae on the basis of the "single" carpel and the "solitary, axillary" flower. It is difficult to understand why these characters were used and emphasized even in the family description because (1) the number of carpels in *Circaeaster*, as shown by the previous descriptions of Hooker (1890), Oliver (1895), Junell (1931), and Janchen (1949), varies from 1-4 and (2) the flowers of *Circaeaster* are not "solitary in the upper leaf-axils," but are clearly united in fascicles which collectively form a condensed inflorescence. Maximowicz (1881), Bentham and Hooker (1883), and Oliver (1895) all drew attention to the fasciculate arrangement of the flowers of *Circaeaster*. In the material which I have studied, the peripheral fascicles consist of 2-many basally united flowers, each group subtended by a bract while the central fascicle consists of a united group of flowers which are clearly devoid of bracts (Figs. 30a-d). Thus on the basis of fluctuation in carpel number and the peculiar morphology of the inflorescence, I am forced to disagree with Hutchinson's description and with his suggestion that *Circaeaster* is "a very reduced relative of the Podophyllaceae or Berberidaceae." The systematic affinities of the Circaeasteraceae appear rather to lie within the Ranales (*sensu lato*). But as is true of a number of monotypic ranalian families recently segregated by Bailey and his associates, positive assertions regarding the evolutionary derivation of the Circaeasteraceae from any existing ranalian family would appear premature and highly speculative at present.

In certain morphological respects, *Circaeaster* seems obviously highly reduced and specialized. Its annual and peculiar rosette-habit of growth, markedly condensed stem and inflorescence and its minute flowers all appear to be strongly derivative characters. But the open and often very symmetrical dichotomous venation is a very puzzling character from a phylogenetic standpoint. Is this distinctive and unusual venation "primitive," or is it the result of "reversion" or "reduction" from a more complex type of foliar vasculature? These are difficult questions, comparable to those which have been raised in discussing the significance of open dichotomous venation in *Kingdonia* (Foster 1959, 1961a, 1961b; Foster & Arnott 1960). But if phylogenetic "reduction" is invoked to "explain" the dichotomous venation of *Circaeaster*, it is difficult to understand why this type of vasculature is not frequently encountered in the small leaves of other specialized dicotyledonous herbs. From a brief survey, using clearing techniques, it is evident on the contrary that relatively complex reticulate venation is characteristic of the small leaves of such genera as *Anagallis* (Primulaceae), *Stellaria* (Caryophyllaceae), *Helxine* (Urticaceae), *Oxalis* (Oxalidaceae), and *Dichondra* (Convolvulaceae). Moreover, in the highly



specialized genus *Raoulia* (Compositae) in which Solbrig (1960) studied the results of reduction on reticulate venation patterns, the "open" venation found in a few species is highly irregular in type and quite unlike the dichotomous venation of *Circaeaster*.

In conclusion, it must be emphasized that remarkably few examples of vein anastomoses were found in the present survey of *Circaeaster* (Figs. 28, 29). Their sporadic occurrence and elemental nature throw no light on the problem of the phylogenetic origin of the dichotomous venation. Likewise, the blind vein endings which were discovered, clearly seem to represent the incompletely developed branches of dichotomized veins and hence do not appear to be "vestiges" of a former reticulate venation pattern (Figs. 23–26). Possibly the striking resemblances between the dichotomous venation patterns of *Circaeaster* and *Kingdonia* are the result of parallel evolution from an ancient and primitive type of angiospermic vasculature. At any event, it is interesting — and perhaps more than coincidental — that the only known authentic examples of open dichotomous venation in the angiosperms occur in two relic genera which grow in comparable environments in the high montane areas of western and southwestern China (see map, Fig. 1). The future comparative study of other herbaceous ranalian dicotyledons in this part of Asia may well yield results of considerable taxonomic and morphological significance.

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## EXPLANATION OF PLATES

### PLATE I

FIG. 5. *Wang 65301* (A). Cleared leaf, photographed with dark-field illumination, showing the very symmetrical type of open dichotomous venation which frequently occurs in *Circaeaster*. Note especially the gradual separation of the two xylem strands below the dichotomy of the central vein.

### PLATE II

FIGS. 6-14. Venation of the cotyledon and various types of primary leaves in *Circaeaster*. 6-11, *Polunin, Sykes & Williams 3412* (BM), foliar sequence in one plant beginning with the univeined cotyledon (FIG. 6) and showing progressive elaboration of dichotomous venation in the primary leaves (FIGS. 7-9) and successive adult leaf types (FIGS. 10 and 11); 12 and 13, *Wang 66252* (A), primary leaves from same plant showing derivation of mid-vein from basal vein dichotomy. 14, *Wang 65301* (A), details of petiolar vasculature of a primary leaf showing origin of mid-vein from union of central branches of two dichotomized xylem strands. Drawing made from cleared leaf photographed with dark-field illumination.

### PLATE III

FIGS. 15-22. Examples of very symmetrical patterns of dichotomous venation in *Circaeaster*, arranged in the order of increasing number of marginal vein-endings. The scale indicates the wide range in size of these leaves. 15-17, *Liu 10678* (WUK), three successive leaves from same plant, illustrating marked regularity of all basal vein-dichotomies. 18, *Junell s.n.* (P), a leaf with 13 vein-endings, from the plant shown in FIG. 3. 19, *Liu 10678* (WUK), a leaf with 14 vein-endings. 20, *Harry Smith 4141* (S), a leaf with 17 vein-endings. 21 and 22, *Soulié 355* (K), two leaves from same plant with respectively 19 and 20 marginal vein-endings. Note short central blind vein-ending in FIG. 22.

### PLATE IV

FIGS. 23-29. Leaves with blind vein-endings or anastomoses. 23, *Stainton, Sykes & Williams 6182* (BM), primary leaf with single lateral blind vein-ending. 24, *Liu 10678* (WUK), leaf with symmetrical dichotomous venation and a single central blind vein-ending. 25, *Stainton, Sykes, & Williams 6182* (BM), leaf with two lateral and one central blind vein-endings. 26, *The same*, leaf with four blind vein-endings; 27, *The same*, leaf showing close approximation of two adjacent veins. 28, *The same*, leaf with anastomosis at left. 29, *Forrest 118* (K), leaf with anastomosis connecting two veins at right.

### PLATE V

FIGS. 30 a-d. Semidiagrammatic transections of a flowering specimen of *Circaeaster* (*Soulié 355*, P) showing the cotyledons, leaves (L) and the inflorescence. The intervals between FIGURES a and b, b and c, and c and d are respectively 16  $\mu$ , 144  $\mu$  and 248  $\mu$ . The flowers in each of the five peripheral fascicles are designated by arabic numerals corresponding to the numbers of



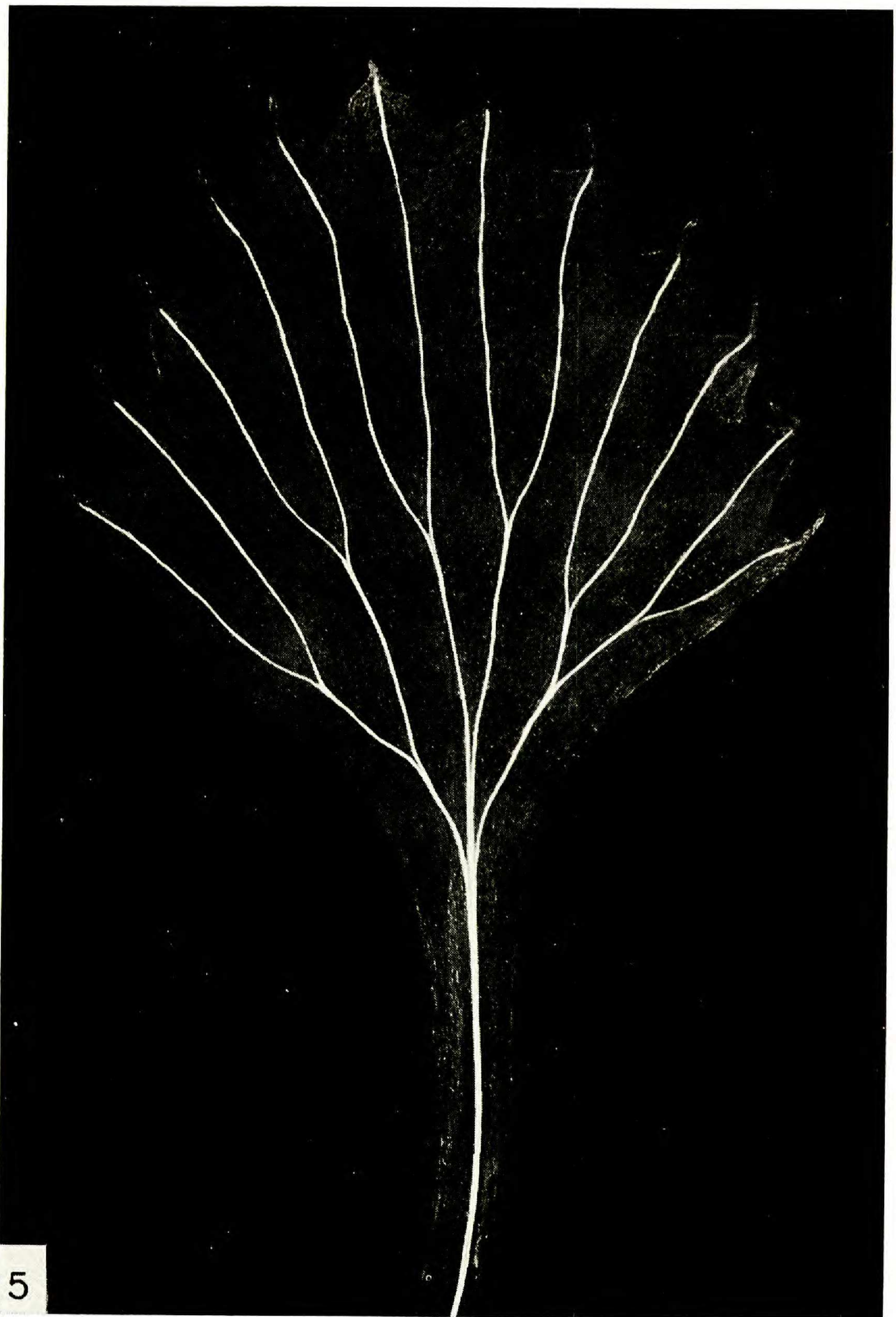
their subtending bracts (B1-B5). The five central ebracteate flowers are indicated by roman numerals (I-V). Note that the xylem (shown in black) in the petiolar bundles usually consists of two closely spaced strands.

Abbreviations for the organs of individual flowers shown in c and d: T, tepal; S, stamen; C, carpel.

#### PLATE VI

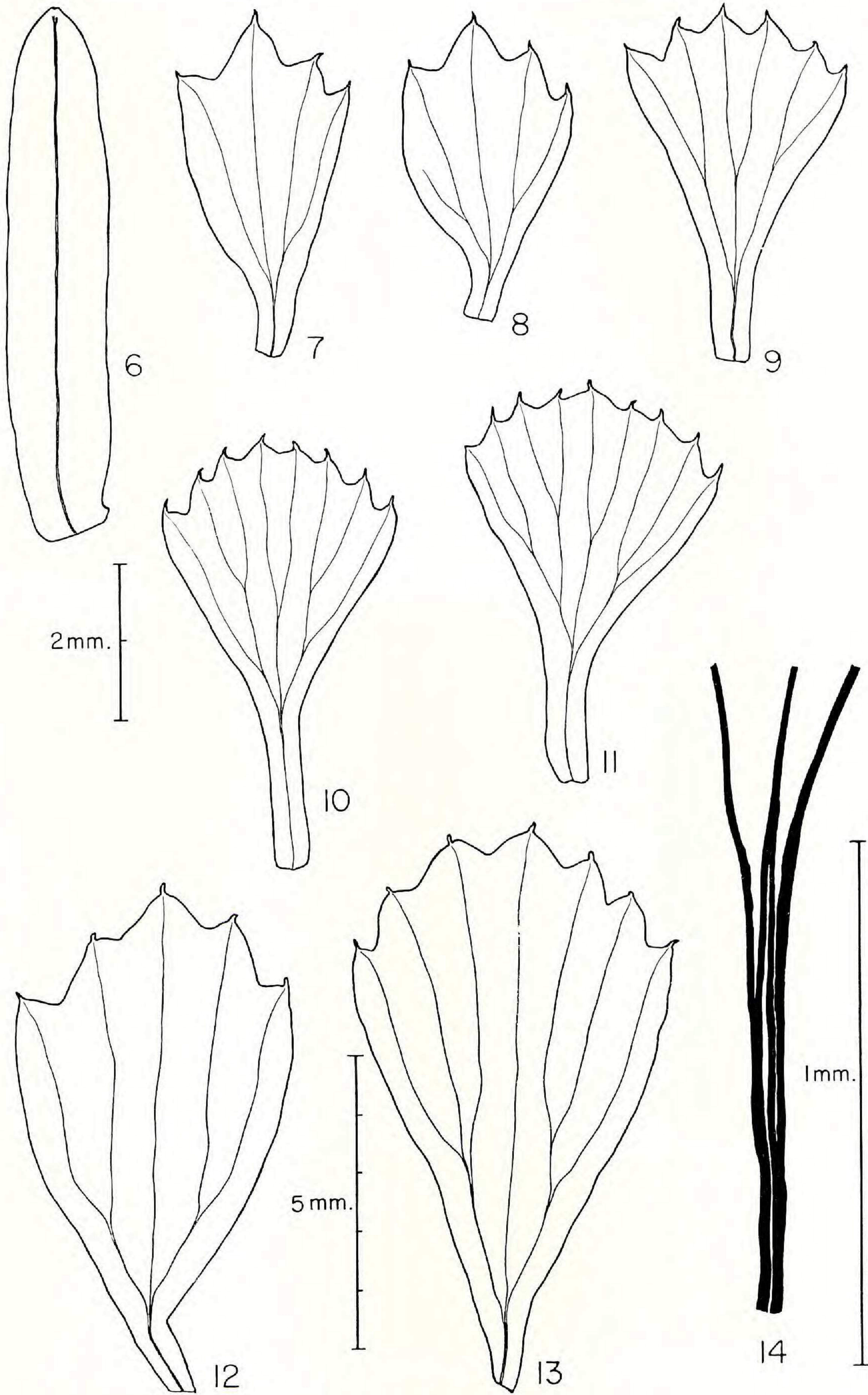
FIGS. 31-35. Morphology of the flower and fruit of *Circaeaster*. Vasculature in all figures shown diagrammatically by broken lines. 31, *Wang 65930 (A)*, at right a fascicle of 3 flowers, the largest consisting of an elongated pedicel, 2 tepals, 2 stamens, and 2 young glabrous carpels; the arrow indicates an enlarged view of the sessile, papillate stigma of one of the carpels. 32, *The same*, older stage of a bicarpellate flower showing the dorsal (left) and ventral (right) veins of the larger carpel and the initiation of hairs. 33, *Polunin, Sykes & Williams 4653 (BM)*, a trimerous flower consisting of 3 tepals, 3 stamens, and 3 carpels; note young hairs. 34-35, *Wang 65930 (A)*, young fruits showing the typical and profuse unciniate hairs; note persistence of stamens with dehiscent anthers. C, carpel; H, hair, P, pollen grain; S, stamen; T, tepal.





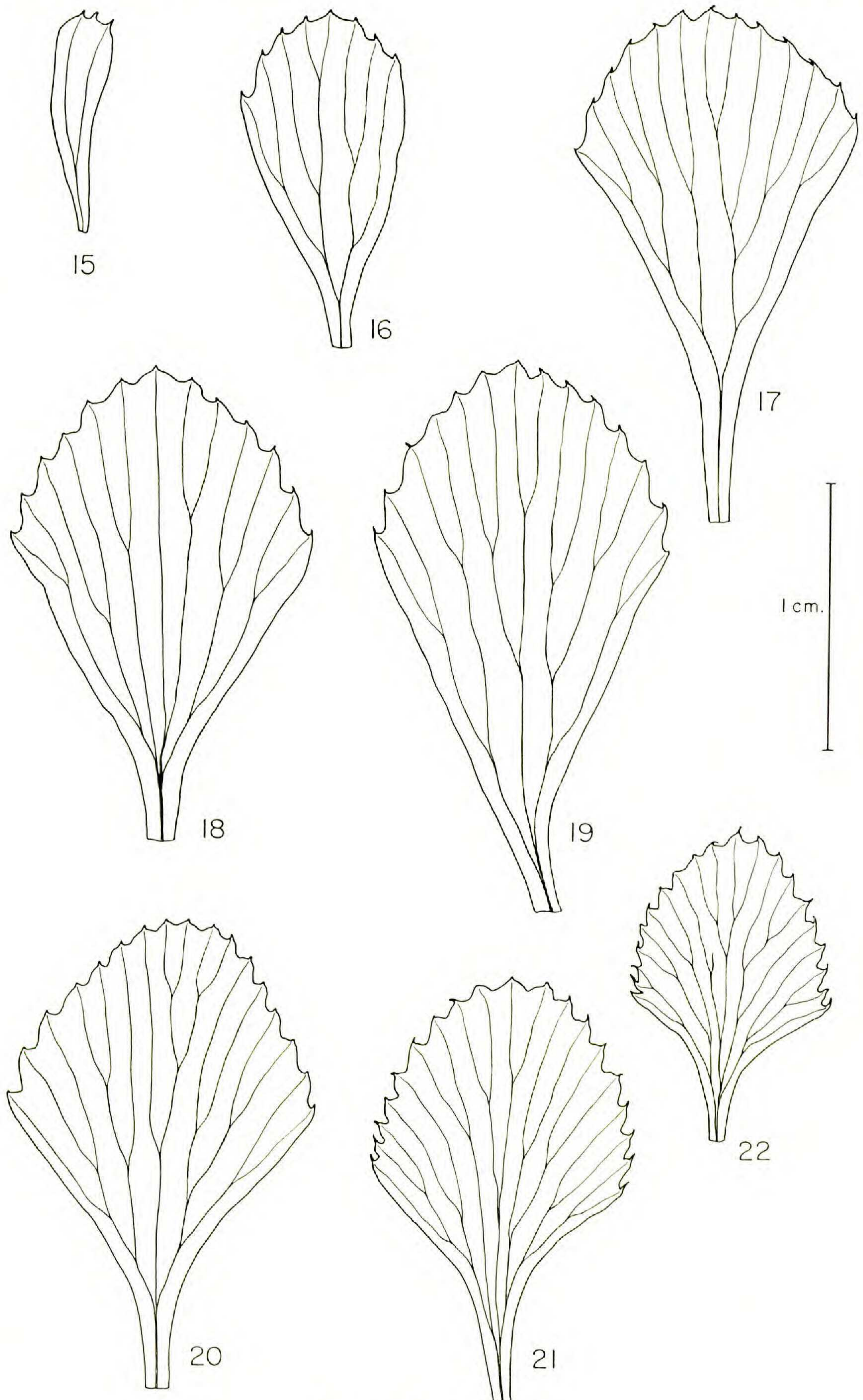
FOSTER, CIRCAEASTER





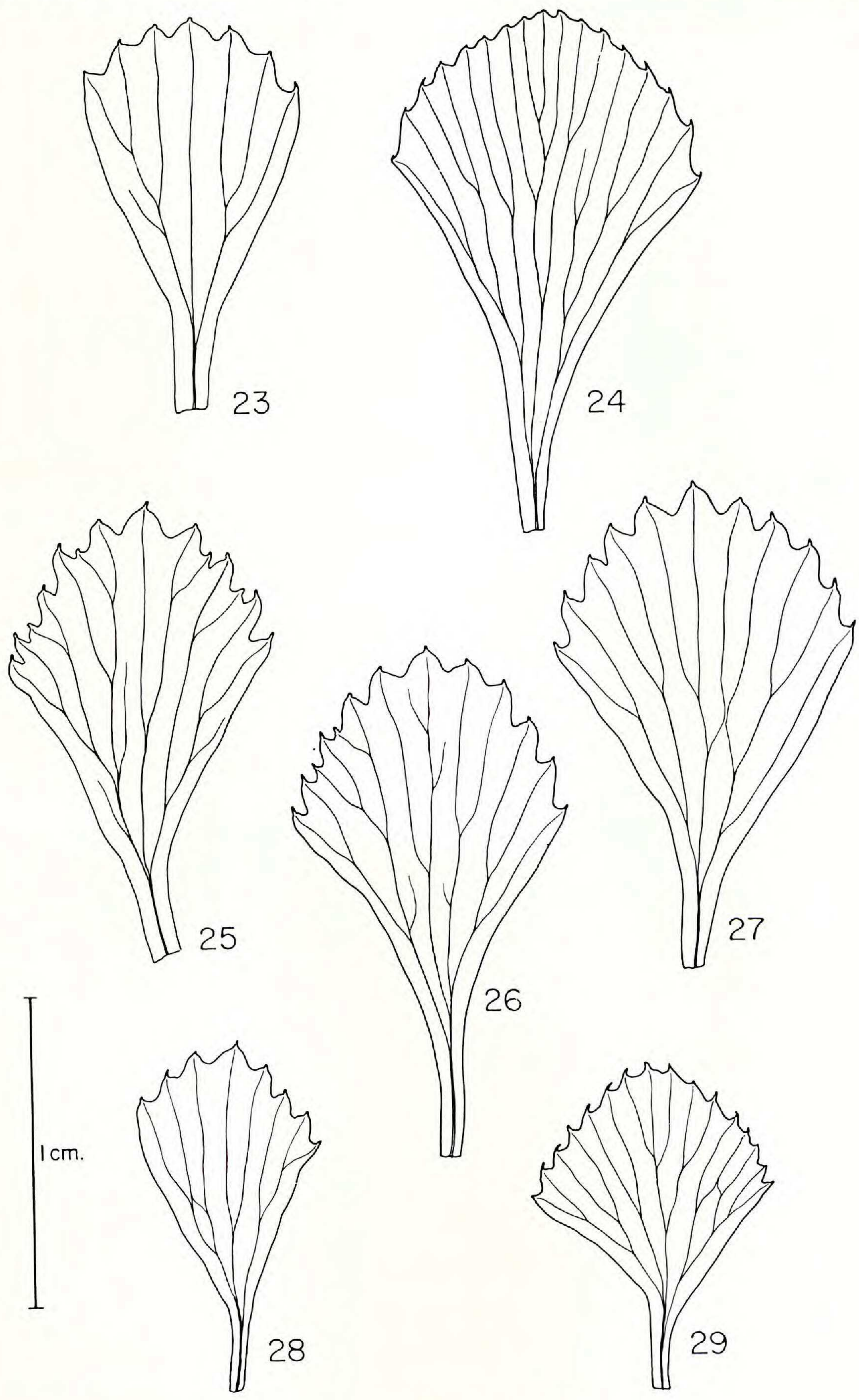
FOSTER, CIRCAEASTER





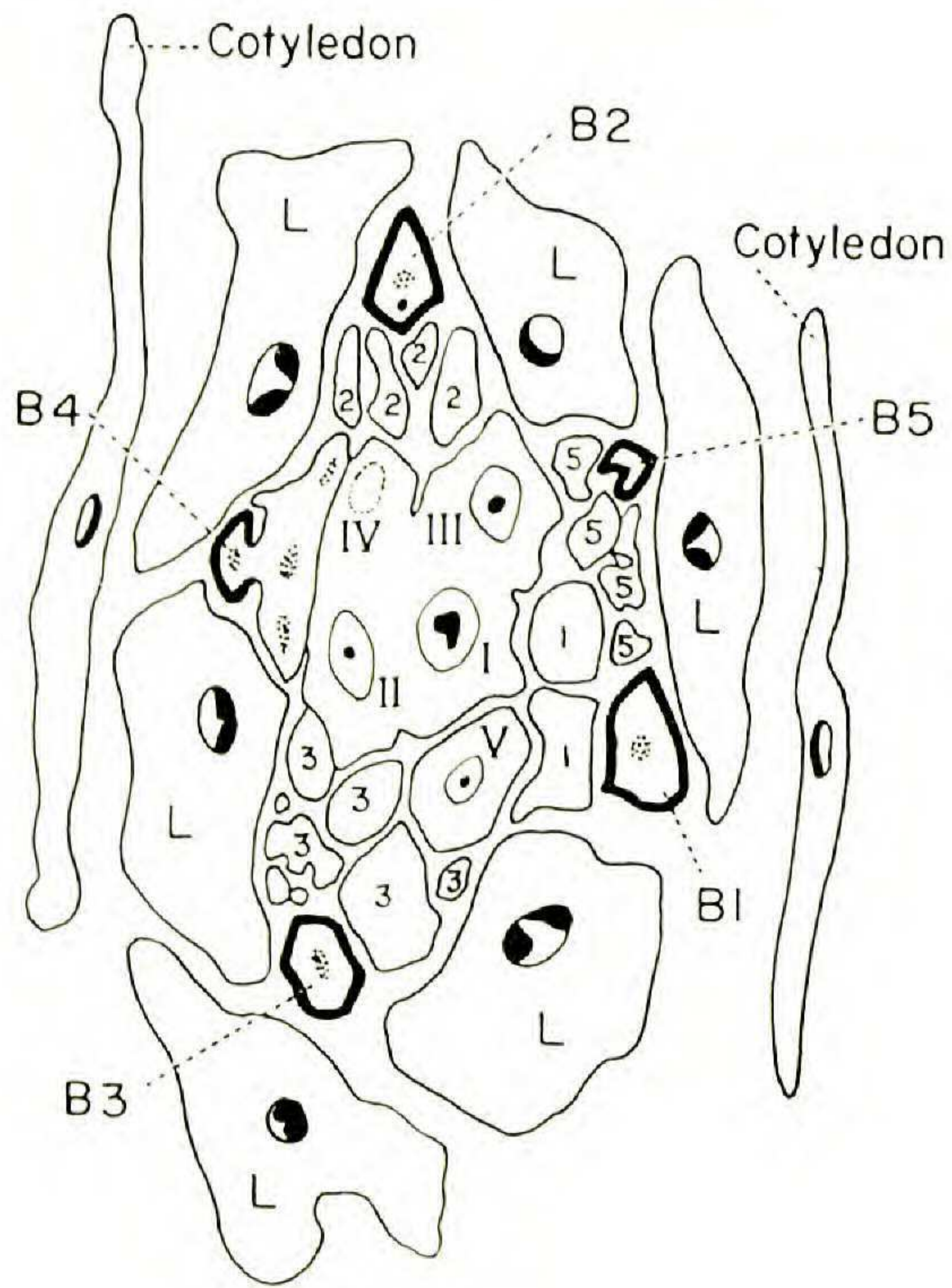
FOSTER, CIRCAEASTER



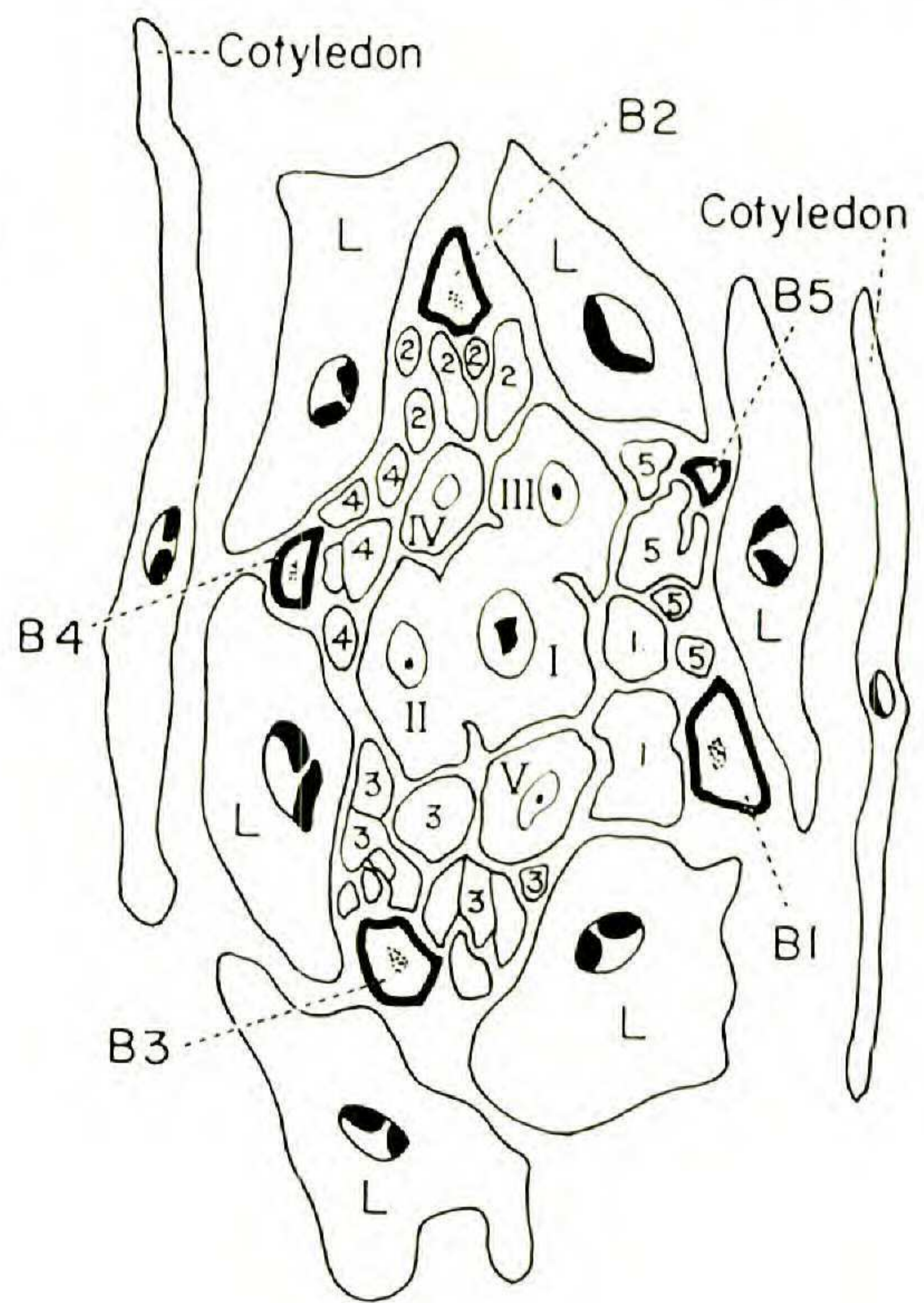


FOSTER, CIRCAEASTER

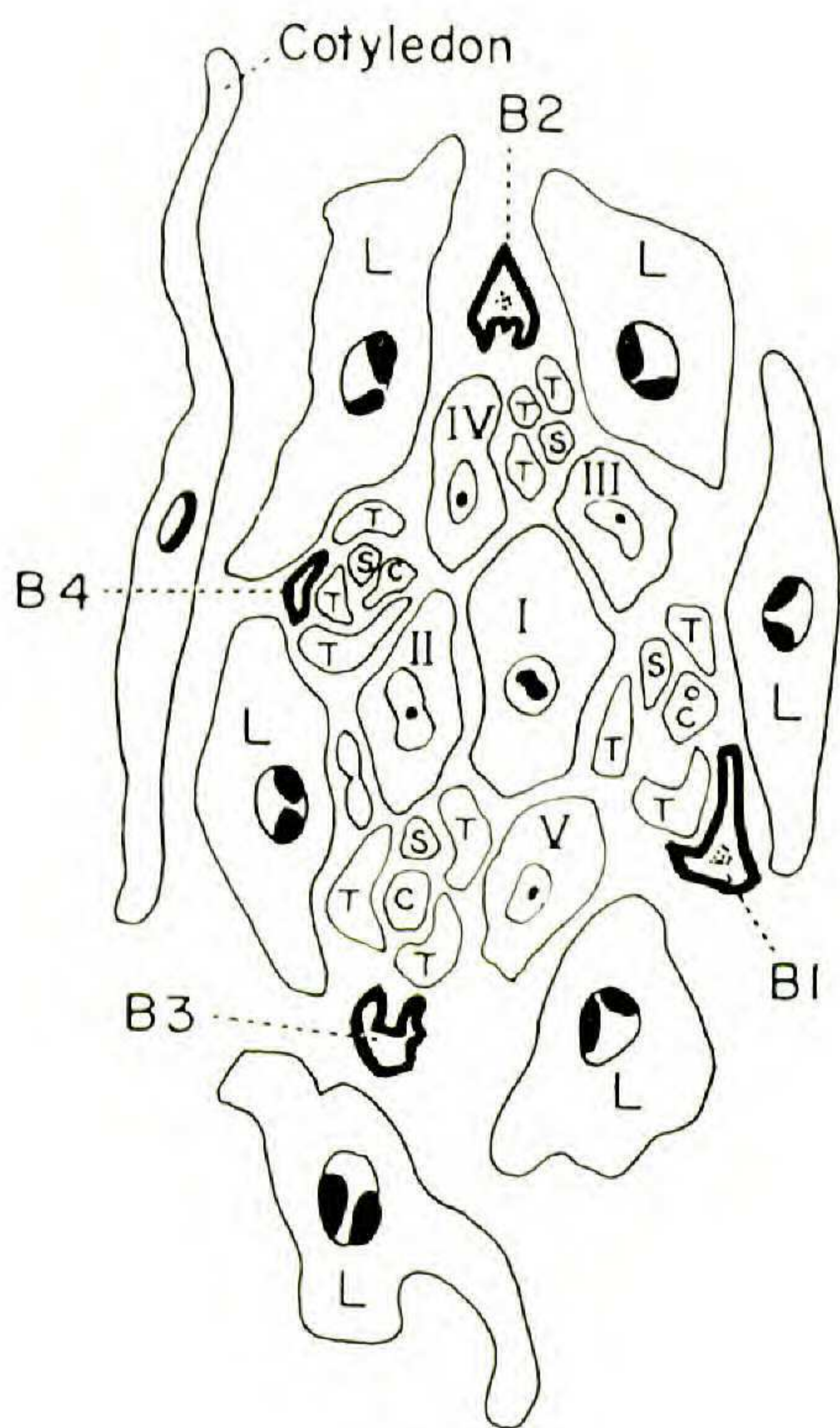




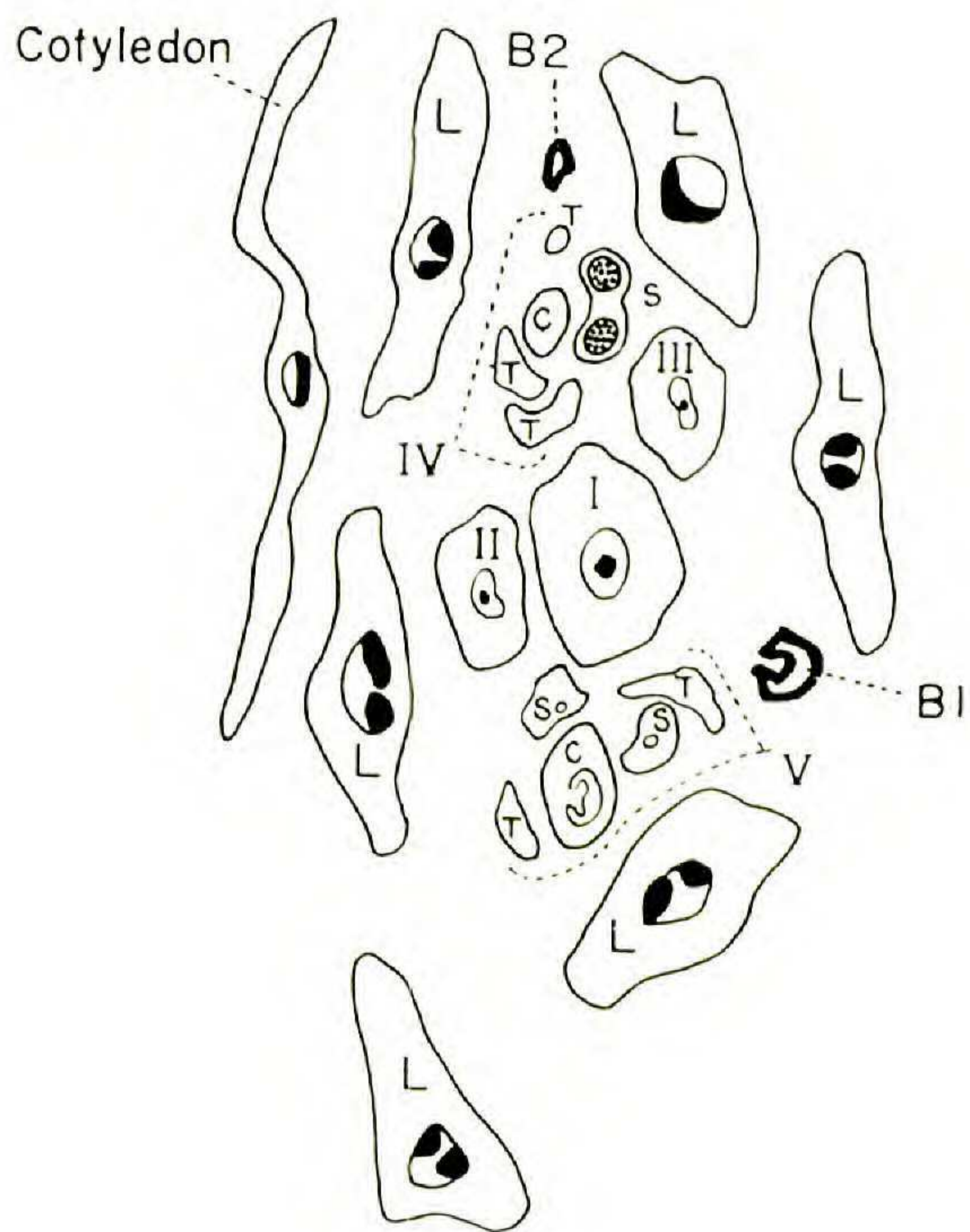
30 a



30 b



30 c



30 d



